# Were the First Insects Terrestrial or Aquatic?

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*Since the time of Darwin, most entomologists have accepted that the ancestors of winged insects were terrestrial, fishmoth-like creatures, a viewpoint which has seldom been challenged. An older, alternative hypothesis argues that ancestral winged insects were aquatic, resembling mayfly larvae. In choosing between these two models, we are not simply evaluating alternative hypotheses; we are contemplating the stem from which all winged insects evolved. Consequently, it makes a profound difference whether we start with a terrestrial or an aquatic organism. In this article, the ruling paradigm is outlined and compared with a tentative alternative, showing how basic assumptions affect interpretations of metamorphosis and the origin of wings. It is concluded that no compelling reasons exist for accepting a terrestrial origin. In contrast, I have been unable to find any evidence incompatible with the aquatic alternative.*

*Sedert die tydvak van Darwin het die meeste entomoloë aanvaar dat die voorouers van gevleuelde insekte terrestriële, vismotagtige diere was, 'n standpunt wat in die verlede selde bevraagteken is. 'n Vroeëre alternatiewe hipotese is dat die voorouerlike gevleuelde insekte akwaties was, en dat hulle 'n ooreenkoms getoon het met eendagsvlieglarwes. Deur 'n keuse tussen die twee modelle te doen, is ons nie slegs besig om die waarde van twee alternatiewe hipoteses te bepaal nie, maar ook om die stam waaruit alle gevleuelde insekte hul ontstaan te danke het in oorweging te neem. Gevolglik maak dit 'n diepgaande verskil of ons òf met 'n terrestriële òf met 'n akwatiese organisme begin. In hierdie artikel word die heersende paradigma in breë trekke geskets, word dit met 'n voorlopige alternatief vergelyk, en word aangedui hoe basiese aannames die interpretasie van metamorfose en die oorsprong van vlerke beïnvloed. Ten slotte blyk dit dat daar geen gebiedende redes is waarom 'n terrestriële oorsprong aanvaar behoort te word nie. Geen bewyse kon gevind word wat met die akwatiese alternatief strydig is nie.*

No fossil insect ancestors have been found or identified,[1-4] so that those which are postulated are necessarily hypothetical. The first fossil winged insects (Pterygota) appear in Upper Carboniferous formations, where a considerable diversity of insect types was already present (Fig. 1). In order to establish the importance of basic assumptions to metamorphosis and wing origin, the generally accepted 'terrestrial model' and a tentative alternative, the 'aquatic model', are outlined below. Subsequently, both are discussed with reference to available evidence.

## The terrestrial model

Most entomologists have accepted variations of this model, which assumes that ancestral Pterygota were terrestrial[4-13] Apterygota,[11,13,14] with open tracheal respiratory systems.[8] This is because it is assumed that all larvae (pre-reproductives) with open respiratory systems can be derived only from ancestors with open systems, so that all groups with larvae that have closed respiratory systems become unacceptable ancestors. As a consequence, wings must have evolved in an animal which had open spiracles in all phases, which means that it must have been terrestrial, because all primitive groups with aquatic larvae, such as Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera have closed respiratory systems.[9,15] This also forces us to accept that all aquatic insects are secondarily aquatic.[5,8]

In the terrestrial model, the origin of wings can be explained according to the 'paranotal theory', which derives wings from fixed tergal (dorsal) expansions of fishmoth-like ancestors.[7,10] These ancestral stages supposedly used their paranotal lobes as gliding aids. Some writers aver that wing articulation then developed *ab initio*. We would also need to accept that muscles became attached to the wings and that these were supplied with motor neurones.

Metamorphosis, according to the terrestrial model, must have originated on land. This follows if aquatic stages with closed respiratory systems are to be avoided. One assumption here is that Endopterygota evolved from terrestrial Exopterygota.[16] Regarding the explanation of why metamorphosis evolved, it has been argued that it developed 'as a mechanism for predator escape (through adult dispersal) or as a mechanism for reducing competition among stages in the life cycle [by evolving two distinct ecological stages]'.[17]

Implicit in the terrestrial model is that endopterygote larval abdominal appendages are all relatively recent developments. For example, Hinton[18] argued that prolegs formed independently at least 27 times in Diptera alone. This conclusion assumes that Endopterygota evolved from terrestrial Exopterygota which lack prolegs.[16,18]

## The aquatic model

Many alternatives to aspects of the terrestrial model have been postulated (e.g. ref. 20), although a comprehensive, non-contradictory explanation has not emerged. The aquatic model is an attempt to develop an independent opposing description of insect origins, and includes the elements of an original explanation for the origin of metamorphosis.

According to this hypothesis, the ancestors of pterygotes were aquatic[19-24] with closed (apneustic) respiratory systems.[20] They possessed two pairs of appendages on all thoracic and abdominal segments.[12,25] Wings were developed during an amphibiotic stage,[12,20,23] according to the 'gill' theory,[12,20] which derives wings from articulated thoracic appendages homologous with the abdominal 'gills' of mayfly larvae. If wings evolved according to the gill theory, one implication is that the ancestors of all winged insects were amphibiotic. Orders such as Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera might all have primarily aquatic larvae.[20] If all winged insects had amphibiotic ancestors and if these larvae are apneustic in all extant amphibiotic orders,[9,15] it would probably follow that larvae with open respiratory mechanisms can evolve from ancestors with closed respiratory systems.[20]

In this model, abdominal appendages such as mayfly and alderfly 'gills' can be regarded as derivatives of primitive appendages, not secondary developments,[12] and larval prolegs can share a common origin with thoracic legs.[10,26]

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If ancestral pterygota were originally aquatic and ametabolous (lacking metamorphosis), all developmental phases would have existed under the same set of selective pressures (Fig. 2*a*). However, when the reproductives left the aquatic environment, larval and reproductive phases would have existed under entirely different selective pressures (Fig. 2*b*). During this stage, wings were developed in the reproductive phase, but apart from this, all stages were morphologically similar. A change in the habitat of larval forms would possibly return all phases to the same selective pressures (Fig. 2*c*) and a 'hemimetabolous' life cycle could be retained. In contrast, groups which remained amphibiotic would continue to exist under different constraints, and phase divergence could develop. If the final pre-reproductive stage left the aquatic environment (Fig. 2*d*), two options would be open. Where wing homologues were present, parallel adaptations to terrestrial life with the adult phase could occur (Ephemeroptera sub-imago?). However, if larval stages had already lost their dorsal appendages, the final pre-reproductive phase would now have a quite different way of life when compared with earlier aquatic larvae and winged reproductives, giving rise to the pupa. Phase divergence would become inevitable if adaptation to these circumstances resulted (Fig. 2*e*). Once metamorphosis had been established, any subsequent change in habitat of one phase would be expected to lead to further phase divergence unless reproductives lost their wings, or larvae developed wings (an improbable event). Metamorphosis can thus be seen as an effect of phase divergence during ancestral amphibiotic life.

## Environmental barriers

Both models imply that a number of environmental barriers have been crossed during the diversification of winged insects. In the terrestrial model, we are forced to accept that terrestrial insects became aquatic on a number of occasions, while according to the aquatic model, larvae became terrestrial a number of times. This provides us with a means of testing the various postulates. If the terrestrial model is incorrect, we should find independent adaptations to terrestrial life in terrestrial larvae. However, if the aquatic model is untenable, independent adaptations to aquatic life in aquatic larvae should be found.

In order to explore these ideas, we need to know where environmental barriers are thought to have been crossed in the two theories. We also need to evaluate the kinds of adaptations that can be expected to have occurred. Unfortunately little is known of comparative larval morphology and physiology, particularly in the most interesting groups from a phylogenetic point of view. However, some environmental barriers have been crossed in the same direction in both models. This allows us to assess some of the effects of major changes in habitat in uncontroversial cases. Both theories accept that aquatic Heteroptera, all aquatic reproductives and some advanced aquatic larvae such as anomalous Lepidoptera are secondarily aquatic.

Independent respiratory adaptations to aquatic life include snorkels (Belostomatidae and Nepidae), 'plastron gills' (Notonectidae and many adult Coleoptera), and organisms which exploit air from aquatic plants. Open respiratory systems, tracheal gills and

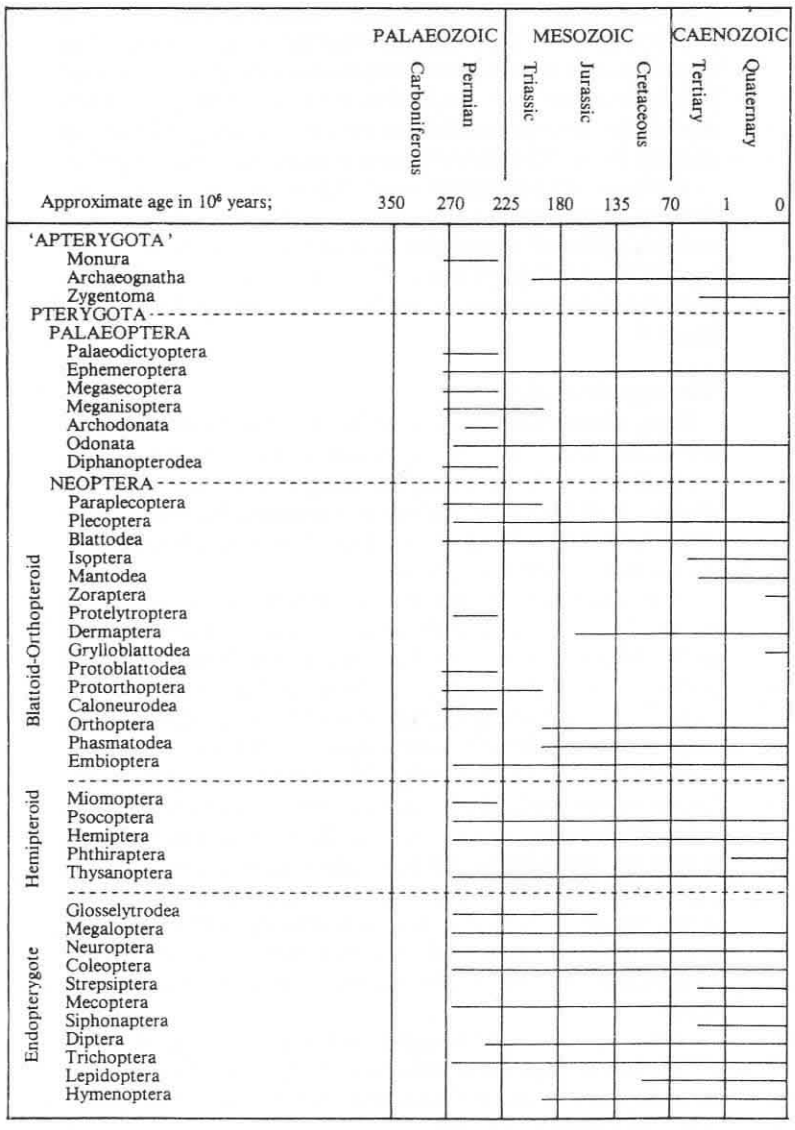


Fig. 1. Fossil history of insects. From Riek,[1] updated according to Rodendorf,[2] Wootton[3] and Hennig.[4]

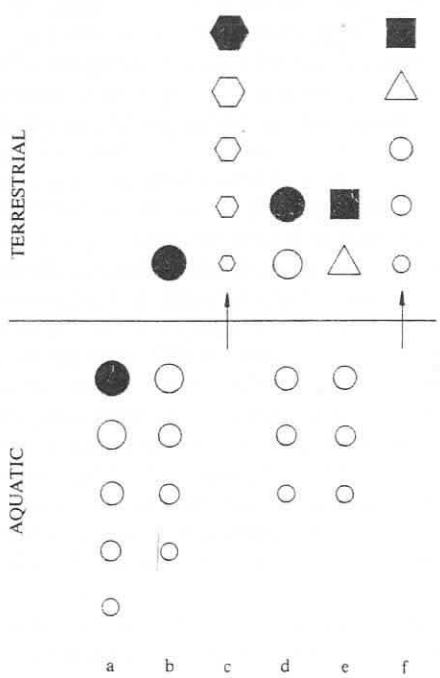


Fig. 2. A scheme suggesting how some of the pterygote groups might have evolved if the first insects were aquatic. Reproductives are shaded black. *a*, Entirely aquatic ancestor; *b*, early pterygote with terrestrial reproductive; *c*, entirely terrestrial Exopterygota; *d*, final pre-reproductive resembles early larval stages but may be terrestrial, e.g. Ephemeroptera, Odonata and Plecoptera; *e*, final pre-reproductive specialized as pupa and highly specialized reproductive, e.g. Megaloptera and Trichoptera; *f*, entirely terrestrial Endopterygota (probably more than once). Differences in the size of symbols represent the growth of organisms. Circles represent the primitive state, with changes to hexagons, triangles or squares indicating specializations.

blood gills are found in Lepidoptera.[27] Almost all positively secondarily aquatic insects retain open respiratory systems and breathe atmospheric oxygen. If these examples of independent respiratory adaptations to aquatic life are compared with the respiratory systems of amphibiotic orders, a sharp contrast emerges. It appears that all these larvae have closed respiratory systems and depend on dissolved oxygen by diffusion.[9,15] This evidence is compatible with the aquatic model, but would need to be accounted for if the terrestrial model is supported.

Terrestrial larvae provide further evidence that conflicts with the terrestrial model, but is anticipated by the aquatic. 'The distribution of functional spiracles varies considerably in different groups of insects, particularly among endopterygote larvae'.[29] This suggests that terrestrial larvae may have acquired independent respiratory adaptations to terrestrial life.

According to the aquatic model, ancestral endopterygotes had amphibiotic ancestors, and their phases diverged because of prolonged adaptation to amphibiotic life. We might thus expect to find differences in adaptations to terrestrial life in different phases. This would explain why 'in the larvae which undergo a perfect metamorphosis (as, for instance, in those of Coleoptera, Lepidoptera, and Hymenoptera) the tracheae are very unlike those of the perfect insect'.[29] In the case of exopterygotes, both phases are thought to have become terrestrial before phase divergence was established. We might then expect to find that larvae and reproductives acquired some adaptations to terrestrial life simultaneously: 'In the larvae of Orthoptera, the tracheae very closely resemble those of the imago'.[29]

## Were ancestral winged insects terrestrial or aquatic?

Although it is often stated, or assumed, that the first insects were terrestrial, reasons why this is so are difficult to find in the literature. One early argument supporting a terrestrial origin is the observation that during early development, 'spiracles' are open.[6] However, since tracheae develop as ectodermal invaginations,[30] what else would be expected? Surely all invaginations begin as indentations or pits which are open at the surface. 'Open spiracles' might therefore represent no more than physical effects of the process of invagination. This does not prove that these 'spiracles' were used previously to breathe air. Ectodermal invaginations in Odonata[31] and Trichoptera[32] do develop as open pits, which illustrates a mechanism that could lead to the development of open spiracles in later instars.

Another argument that has been used to support a terrestrial origin is that 'spiracles' of mayfly larvae are said to function during ecdysis.[8,33] This does not prove that their original function was respiratory. Furthermore, this argument is questionable. Landa,[33] who worked mainly on later instar larvae, did not comment on Lubbock's[34,35] earlier contradictory observation that 'another unusual fact connected with the tracheae of *Chloëon* is that their internal chitinous envelope is not shed with the skin. . . When, however, the insect changes into the proimago and quits the water, spiracles are formed; and at this moult, for the first time, the inner skin of the tracheae is cast, as is the case in other insects.' So little is known about the early ontogeny of mayflies, that it seems Lubbock's work is the most recent study published in English! In an amphibiotic group where larvae do shed their tracheal linings during ecdysis, this suggests a mechanism that could lead to the development of open spiracles in earlier instars,[20,36] since spiracles would be open during shedding.

Early ontogeny of mayflies might provide additional data on this matter. These are needed, because few clues are available from other areas. For example, the fossil record shows that both terrestrial and amphibiotic orders were probably present in the Upper Carboniferous, which tells us only that they had already diverged.

Since Gegenbaur,[20] attempts to explain how tracheae originally developed are rare. Gegenbaur thought that open respiratory systems evolved from closed systems found in aquatic larvae such as mayflies. Later,[37] he was led to believe that the first insects were terrestrial, but continued to invoke the 'gill' theory to explain the origin of wings.

Whether we accept a terrestrial or an aquatic origin, the assumption that the original function of these ectodermal invaginations was respiratory, seems to lead to the unacceptable conclusion that 'foresight' was involved. Until an invagination has developed, it can have no respiratory advantage, but before it develops, an imaginal disc must be present. An alternative to invoking foresight is the possibility that these invaginations originally served some other function, which pre-adapted them to develop as respiratory organs. Air inside these 'tracheal precursors' would presumably increase buoyancy during aquatic life. This avoids postulating the *de novo* development of tracheal imaginal discs in the first terrestrial insects.

Until we know more about the early ontogeny of respiratory systems in Ephemeroptera and Megaloptera, we can only speculate about possible pre-adaptive functions of respiratory systems. Tracheal tubes are present in exopterygote larval wing buds, before the veins of the reproductive wings are formed.[38] This could be interpreted as evidence that wings developed from tracheated appendages which were not used for flight (such as gills).[20] Since tracheae develop as ectodermal invaginations it seems possible that they could have been derived from invaginations that were already present in a distant aquatic ancestor. Embryonic evidence suggests that the onycophoran-myriapod-hexapod assemblage is a unitary phylogenetic group, and that 'at the very least',[39] onycophorans are related to the segmental ancestors of annelids. Annelids and insects must therefore have shared a common ancestor, and the origin of ectodermal invaginations in these groups would be interesting to investigate. Polychaete chaetal sacs and nephridia develop as ectodermal invaginations, the latter having been 'sadly neglected by embryologists'.[39] Further data on annelid and insect ectodermal invaginations are therefore needed before any conclusion can be reached.

## Can open spiracles be derived from closed systems?

One of the contrasting expectations of the two models concerns the respiratory systems of aquatic larvae. According to the terrestrial model, open respiratory mechanisms cannot be derived from closed ones. In contrast, the aquatic model suggests that they can. This would make comparative studies of the respiration of aquatic and related terrestrial larvae particularly interesting. For example, Trichoptera and Lepidoptera are considered to be closely related[4,40] and Crowson[41] thinks that Coleoptera arose from megalopteran or megalopteran-like ancestors.

Recent studies on the embryonic development of primitive Lepidoptera (Micropterygidae) provide additional evidence that they are closely related to Trichoptera.[42] According to the fossil record, Trichoptera were present about 100 million years before the appearance of Lepidoptera. This is not a reliable way of dating the origin of these orders, but there is certainly no proof that Lepidoptera are as ancient as Trichoptera.[4] In the terrestrial model it is necessary to assume that Lepidoptera are at least as ancient as Trichoptera, while in the alternative model they could be relatively recent. A crucial test between the two models might be possible here. In the aquatic model open respiratory systems of primitive lepidopterous larvae could be derived from closed systems in Trichoptera, while in the terrestrial model this would be impossible. Once again, further data on the ontogeny of respiratory systems are required.

A comparative study of respiratory systems in Megaloptera, Coleoptera and Neuroptera might prove equally instructive. Crowson's opinion that Coleoptera arose from megalopteran or megalopteran-like ancestors is compatible with the aquatic model, and quite incompatible with the terrestrial hypothesis. The anomalous neuropteran family Sisyridae could also be helpful to study. Their larvae are unique in a number of ways, if compared with other neuropteran larvae. Not only are they aquatic, but they

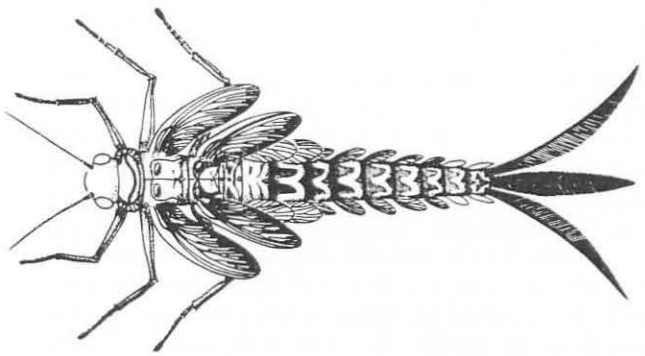

Fig. 3. Larva of the mayfly *Protereisma americana* from the Lower Permian, which supports the gill theory of the origin of wings. Reproduced from Hubbard and Kukalová-Peck[54] with permission of authors and publisher.

possess segmented abdominal appendages.[43] In the terrestrial model we would have to accept that these appendages developed *de novo* in response to a secondary return to water. In contrast, the aquatic model allows that they could have been acquired from megalopteran ancestors, which suggests that these larvae could also be primarily aquatic.

## Can Pterygota be derived from Apterygota?

According to Manton,[44] Pterygota cannot be derived from Apterygota because they differ in limb and mandibular morphology and articulation. Some of Manton's views may need to be re-assessed now that 'Thysanura' are considered to be an unnatural group, and Zygentoma are regarded as the closest 'apterygote' relatives of winged insects.[4,40] If we are to accept that Zygentoma are ancestral to, or equally ancient with Pterygota, as the terrestrial model suggests,[4] we would need to accept or explain a 260-million year gap in the fossil record as it stands (Fig. 1).

There is no compelling evidence that pterygotes evolved from apterygotes. This does not mean that they did not share a common ancestor, but it cannot be argued that ancestral Pterygota were terrestrial on this basis.

## Evidence for the origin of wings

At present, we lack evidence of meso- or metathoracic paranotal lobes in any group from which Pterygota can be derived with confidence. However, there is fossil evidence to support the gill theory. Fossil mayfly larvae such as *Protereisma americana* (Fig. 3) indicate that larval wingpads were articulated,[12,45] and that they probably were serial homologues of 'gills'.[12]. This also supports an amphibiotic origin of wings, and indicates that ancestral pterygotes may have been aquatic. There is no obvious advantage in invoking a terrestrial stage to precede this aquatic stage as a number of authors have done.[12,14,37] Since all primitive groups with aquatic larvae have closed respiratory systems, an amphibiotic origin implies that open respiratory systems can occasionally develop from closed ones.

According to the aquatic model, the first terrestrial reproductives already possessed articulate (tracheated?) appendages that were to give rise to wings, which were supplied with muscles and motor neurones. One of the problems of terrestrial life is that temperatures fluctuate much more than in water. It has been postulated that pro-wings could have functioned as thermoregulatory devices before the first flight.[46,47] The use of these structures for cooling by creating air currents would facilitate increase in size and the development of muscles.

## Missing fossil ancestors

The sudden appearance of a 'chaotic array'[3] of fully winged insects in the Upper Carboniferous demands an explanation. Although no compelling explanation has emerged in the terrestrial model, a simple explanation follows as a logical consequence of the aquatic model. If the first insects were aquatic, all early stages of insect evolution could have occurred in a single fresh water location. Until this habitat was located, no fossils would be found because aquatic and early amphibiotic insects would lack any effective means of dispersal until wings were fully dveloped. Even the first terrestrial reproductives would be restricted in their terrestrial excursions until they had developed adaptations to terrestrial life. One effect of the possession of wings would be an efficient means of dispersal which would lead to a wide distribution and, for us, the discovery of fossils in many localities.

The dispersal of primitive archetypal pterygotes, imperfectly adapted to any terrestrial habitat, would lead to independent specializations of wings and other terrestrial adaptations in any locality where small populations were established. This would lead to rapid diversification, or 'explosive evolution'.

## Cause and effect in interpretations of metamorphosis

In the terrestrial model, it has been argued that metamorphosis developed because it conferred certain functional advantages. Observation tells us that reproductives disperse far more efficiently than larvae, simply because they can fly. We also know that endopterygote reproductives generally exploit entirely different food sources from their larvae. However, that these characteristics are the original causes of phase divergence has yet to be demonstrated. Indeed, they could be *post facto* explanations.

According to the aquatic model, metamorphosis is simply an incidental effect of phase divergence in adaptation to differing selective pressures during ancestral amphibiotic life. Reference to the fossil record shows that orders with terrestrial larvae, such as Lepidoptera, and Hymenoptera, where dramatic transformations occur, are evidently more recent than amphibiotic endopterygotes such as Megaloptera and Trichoptera. In cases such as Mecoptera, Neuroptera, Coleoptera and Diptera, both terrestrial and aquatic larvae exist, but it would be premature to assert that any of these are primarily or secondarily aquatic before their status has been carefully evaluated. It is also possible that some primarily aquatic larvae might possess open respiratory systems.

## Are endopterygote larval appendages all secondary developments?

According to Hinton,[18] endopterygote prolegs are all relatively recent formations. If this were true, we might expect to find no evidence of a common origin in the genetic basis of appendage development. Indeed, Hinton[18] maintained that in Diptera alone, prolegs have evolved at least 27 times. This implies that 'proleg development genes' must have evolved independently at least 27 times, and that these should never show any phylogenetic relationship with the genes for thoracic legs. Recent developments in cell biology indicate that an exciting new line of evidence is now available. Some workers think that homeotic mutations in *Drosophila* show that wing homologues were previously present on abdominal segments of ancestral insects.[48] Since these mutations can produce both abdominal legs and abdominal wing homologues,[48,49] they could support the view that archetypal insects possessed two pairs of appendages per segment. It is also evident that some mutations which affect the morphology of reproductive thoracic legs also affect the morphology or distribution of larval prolegs (e.g. extra sex-combs).[50] This is interesting because it suggests that even in some highly advanced insects, there may be common genes affecting larval and reproductive appendages.

Additional evidence supporting the view that ancestral insects possessed abdominal wing equivalents comes from the discovery that interneurones involved in the generation of motor activity for flight in locusts are also present in the first three abdominal segments.[51] This finding can be accommodated in the aquatic model, where these interneurones could have served abdominal wing homologues in ancestral forms. In the terrestrial model the function of these interneurones might prove difficult to explain.

If ancestral Pterygota possessed two pairs of appendages on each segment, we might find evidence for these features in early embryonic development. Miyakawa has recently found that during the early development of *Protohermes grandis* (Megaloptera) two pairs of swellings appear on the abdominal segments. One pair gives rise to 'tracheal gills' while the other pair disappears.[52]

Another observation which is incompatible with the terrestrial model, but anticipated in the aquatic model, is that vestigial 'gills' are found in some primitive mayfly and dragonfly adults.[36] If gills were actually derived adaptations to aquatic larval life, this could be difficult to explain.

With the terrestrial model, we are faced with the problem that primitive insects such as Ephemeroptera and Megaloptera have highly derived larvae. Hennig[4] regarded alderfly 'gills' as derived features, but found 'unfortunately, it is almost impossible to recognize any characters in the ground plan of the adult as being definitely derived'. However, 'with proper evaluation it must always be possible to bring larval and imaginal [phylogenetic] systems into congruence'.[53] In contrast to this the expectation from the aquatic model is that primitive appendages will be found in primitive groups. Apparently, dorsal abdominal appendages have been lost in Megaloptera, whereas ventral abdominal appendages, with the possible exception of genital appendages, have been lost in living Ephemeroptera. Thus, both mayfly and alderfly 'gills' are seen as modified abdominal appendages inherited from a common ancestor.

Although the terrestrial model has been generally accepted by entomologists, it is shown here that its foundations are not secure. Refutation of aspects of either terrestrial or aquatic model could lead to their modification, or even to the rejection of one or both. This would considerably strengthen the theoretical foundations of entomology. All available evidence cannot be explained by the terrestrial model at present. In contrast, it appears that the aquatic alternative is compatible with the available evidence.

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The sequel to this article, 'Environmental selective pressures and the origin of insect metamorphosis', which refers to further pertinent papers, has been accepted for publication by the *Journal of the Entomological Society of Southern Africa.*